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Review Article

Opportunistic habitat use: widespread and non-threatened anurans in Brazilian caves

Vinícius da Fontoura Sperandei[1,2], Wilian Vaz-Silva[3], Cássio Cardoso Pereira[4], Francisco Leonardo Tejerina-Garro[1,3,5]

1 *Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, 13565-905, Km 235, Rodovia Washington Luís, São Carlos, São Paulo, Brazil*
2 *Universidade de Rio Verde, Fazenda Fontes do Saber, 75901-970, Rio Verde, Goiás, Brazil*
3 *Programa de Pós-Graduação em Ciências ambientais e saúde, Pontifícia Universidade Católica de Goiás, Av. Universitária 1.440, Setor Universitário, 74605-010, Goiânia, Goiás, Brazil*
4 *Programa de Pós-Graduação em Ecologia, Universidade Federal de São João del-Rei, 36307-352, São João del-Rei, Minas Gerais, Brazil*
5 *Programa de Pós-Graduação em Sociedade, tecnologia e meio ambiente, Universidade Evangélica de Goiás, 75083-515, Av. Universitária km 3,5 Cidade Universitária – Anápolis, Goiás, Brazil*

Corresponding author: Vinícius da Fontoura Sperandei (vinicius.sperandei@gmail.com)

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Abstract

Anurans are highly sensitive vertebrates whose ecological distribution is strongly shaped by environmental conditions, particularly moisture availability and habitat stability. Although most species are associated with epigean environments, several anurans use subterranean habitats, such as caves, as shelters, refuges, or complementary habitats. Caves represent unique ecological environments in Neotropical landscapes and are characterized by high environmental stability, acting as ecological filters that select for species capable of utilizing them. Because anurans typically depend on humid environments and are predominantly nocturnal, they are potential users of subterranean environments. In this study, we evaluated how taxonomic variables (species and family) relate to the conservation status, geographic distribution, and life-history traits of anurans recorded in natural caves in Brazil. For this purpose, 177 occurrence records for 54 species were compiled from the scientific literature. The species were characterized by their conservation status, distribution range, endemism, and life-history attributes (period of activity, habitat frequency, and mating site). The data were analyzed using redundancy analysis (RDA). The results indicate that geographic and conservation-related variables (conservation status, distribution range, and endemism) are the main predictors of anuran occurrence in caves. The predominance of widely distributed anurans classified as IUCN Least Concern suggests that their use of caves is opportunistic, with caves functioning primarily as refuges or as complements to surface habitats. These findings indicate that cave use by anurans is largely driven by ecological plasticity rather than specialization to subterranean environments, and, by compiling and analyzing records from across Brazil, this study provides the first macroecological synthesis of cave-associated anurans in the country, highlighting important sampling gaps and reinforcing the need to systematically incorporate amphibians into research and conservation policies for Neotropical subterranean ecosystems.

Key words: Cave biology, conservation biology, herpetofauna, life history, neotropical karst, speleology

Introduction

Amphibians are vertebrates highly sensitive to environmental variation due to their permeable skin, dependence on moisture, and strong coupling with both biotic and abiotic factors throughout their life cycle (Bernarde 2012; Dos Santos et al. 2022; Sperandei et al. 2025). Among them, anurans are of particular interest because of their high species richness and ecological plasticity across different environments. These characteristics make them especially responsive to environmental filters that shape their distribution and habitat use. Within ecological systems, individuals are part of complex networks of biotic and abiotic interactions that influence their survival and persistence in specific habitats, and certain environments may provide favorable conditions for key life activities (Culver and Pipan 2019).

The Neotropical Brazilian epigean environment stands out for its high species richness of anurans, with 1,144 species recorded (Segalla et al. 2022). This taxonomic group generally occurs in a wide range of environments, exhibits predominantly nocturnal habits, and displays considerable dietary plasticity (Dodd 2010; Bernarde 2012; Lima et al. 2012a). In addition to the species richness of anurans, Brazil has a high density of caves and the potential to reveal a higher number of natural caves in the Neotropical region due to the vast extent of soils and rocks susceptible to speleogenesis, many of which remain unexplored or unsurveyed (Piló and Auler 2011; Jansen et al. 2012; Segalla et al. 2022). Natural subterranean change for environment provide favorable refuges for amphibians due to their high and relatively stable humidity, reduced temperature fluctuations, and low light incidence—conditions that help prevent exposure to visually oriented predators and skin desiccation (Eterovick et al. 2010; Matavelli et al. 2015). These conditions also support other fundamental activities in the anuran life cycle, such as feeding, given the wide diversity and abundance of invertebrates in caves (Bernarde 2012), and reproduction, since watercourses are often present.

Well-defined abiotic characteristics with high stability are hallmarks of the cave environment (Culver and Pipan 2019). Natural caves exhibit a permanent absence of direct sunlight in their deeper zones. Light intensity demarcates the developmental zones of the cavity, creating a gradient from the cave entrance (entrance or photic, disphotic, and aphotic zones), while temperature remains stable and relative humidity approaches saturation (Culver and Pipan 2009; Mejía-Ortíz et al. 2021). Other characteristics that also shape the cave environment include resource scarcity and the energy input to the cave ecosystem, which is predominantly of epigean origin and consists of detritus or dissolved organic matter carried by water, wind, or animals transiting between hypogean and epigean environments (Culver and Pipan 2009; Silva et al. 2012; Souza-Silva and Ferreira 2022). These attributes collectively limit the occupation of the subterranean environment by most surface-dwelling species, acting as an environmental filter (Gibert and Deharveng 2002). The ecological structures of subterranean caves typically form simplified trophic networks (Poulson and Lavoie 2000; Poulson 2012), primarily based on detritivores and invertebrates.

The cave fauna comprises species that can inhabit this environment either temporarily or permanently, and this relationship determines their biospeleological classification for conservation and research purposes (Sket 2008; Sperandei et al. 2023). The categories, originally proposed by Schiner-Racovitza (1907) and adapted by Sket (2008), define how species transit between epigean and

hypogean environments and their dependence on the subterranean environment for survival. Troglobites, obligate cave dwellers, are animals exclusive to the subterranean environment, often exhibiting morphophysiological and behavioral modifications. Troglophiles, with an affinity for the cave environment, are species that can occupy it without dependence and form populations in epigean habitats as well. Trogloxenes, transients between surface and subterranean environments, are animals that inhabit hypogean environments at some point for refuge, nesting, or reproduction but must periodically return to the external environment to complete their life cycle. Additionally, there is the classification of accidental animals, which inadvertently enter a cavity but lack the capacity to obtain food to remain for long periods, thus either leaving or dying inside the cave if they cannot overcome physical obstacles (Sket 2008; Culver and Pipan 2009).

Among vertebrates found in cave environments, fish and bats have the most extensive scientific literature, while amphibians have been studied mainly in cases involving salamanders in Europe and Asia (Romero Díaz 2009; Lunghi et al. 2018; Turbanov et al. 2019). The taxonomic group of anurans has received increasing attention, thereby expanding the global scientific understanding of subterranean vertebrate ecology in recent years. Reports and studies indicate the systematic use of subterranean habitats by anurans, primarily in response to extreme climatic variations on the surface (Luría-Manzano et al. 2017; Suwannapoom et al. 2018; Couto et al. 2023).

Because they are classified as accidental fauna, anurans are not protected under current Brazilian environmental legislation for subterranean environments (Brasil 2008; Ministério do Meio Ambiente 2017), and there is consequently no legal obligation to record or collect them in caves. Recent studies also question whether caves function merely as favorable rocky environments or as true habitats for anurans, noting that many species regularly use these environments rather than occurring there purely by chance (Sperandei et al. 2023). This lack of legal recognition contrasts with groups explicitly mentioned in the legislation, such as bats, fish, and invertebrates, which have formed the basis for many studies advancing research on subterranean biology since Brazilian Federal Decree 6640 (Brasil 2008). Given the high species richness of Brazilian anurans, their ecological plasticity, and their recurrent use of subterranean habitats, it is important to systematically assess their occurrence in caves. Existing legislation and research practices result in their significant underrepresentation, limiting our understanding of the factors that influence their cave use. Despite progress in the study of subterranean fauna, herpetofaunal research remains marginal, even though informal observations and cave visits frequently result in sightings or occasional encounters with these animals. Consequently, there is currently no comprehensive synthesis evaluating the ecological and biogeographic patterns associated with anuran occurrence in Brazilian caves.

This study presents a systematic review of the literature on the occurrence of Brazilian anurans in natural caves. We aimed to identify patterns and key factors associated with their presence, focusing on variables related to conservation status, geographic distribution, and life history traits. By compiling and analyzing published occurrence records, we sought to highlight how biological and ecological characteristics of anurans influence their use of subterranean habitats, identify gaps in current knowledge, and provide guidance for future research and conservation efforts in Brazilian subterranean environments.

Methods

Data collection

A search for scientific records of anurans observed within natural caves in Brazil was conducted using Google Scholar (https://scholar.google.com), Scopus (www.scopus.com), and the Web of Science (www.isiknowledge.com). Searches included all records available in each database from their earliest coverage through 15 December 2022. The combination of multiple databases was performed to include the widest possible range of literature, encompassing available theses, dissertations, book chapters, and peer-reviewed articles from journals indexed on these platforms (Martín-Martín et al. 2021), following the PRISMA guidelines for systematic literature searches (Page et al. 2021) (Fig. 1).

Keywords were used both independently and in combination in English (*Anura*, Brazilian caves, anurans, amphibians, toads, subterranean cavities, subterranean habitat, underground environment, cave, grotto, burrow) and in Portuguese (*Anura*, cavernas brasileiras, anurans, anfíbios, sapos, cavidades subterrâneas, habitat subterrâneo, ambiente subterrâneo, caverna, gruta, toca). Records of anurans lacking identification to the species level were excluded, and only those with complete taxonomic identification were considered (Fig. 1). The nomenclature of each species was verified and updated when necessary, following "Amphibian Species of the World", version 6.1 (Frost 2025).

Afterward, information on the conservation status of each species was collected. We considered the International Union for Conservation of Nature (IUCN) Red List status (IUCN 2024) and the Brazilian classification by the Brazilian Ministry of the Environment (Ministério do Meio Ambiente – MMA) (Ministério do Meio Ambiente 2022). Both systems use the same categories: Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, and Extinct. The Brazilian conservation list was included because some species are classified under a different conservation status than in the IUCN list.

The geographic distribution of species was characterized by three variables: species distribution area, endemism, and frequency of occurrence. Species distribution area refers to the total region occupied by a species, and in this study it was classified as restricted (one or two Brazilian states), moderate (three or four states), or widespread (more than four states). The number of states with confirmed records was used as an operational proxy for distribution breadth because detailed spatial data on the actual occupied area of many anuran species remain incomplete. Using the total area of states (km^2) could overestimate distribution ranges, particularly for species recorded from only a few localities within large states. Therefore, the number of states was adopted as a standardized and reproducible measure of geographic distribution based on documented occurrence records. Endemism denotes whether a species is exclusive to a specific geographic region (Gaston 2003), and here it was classified as yes or no. Frequency of occurrence reflects how often a species is observed within its distribution area and is classified as infrequent (species observed only occasionally, with low detectability or dependent on specific conditions and, although present in the area, not consistently recorded), frequent (species recorded regularly, with high density or detectability, occurring widely and predictably in the habitat), or rare (species recorded only exceptionally, with few

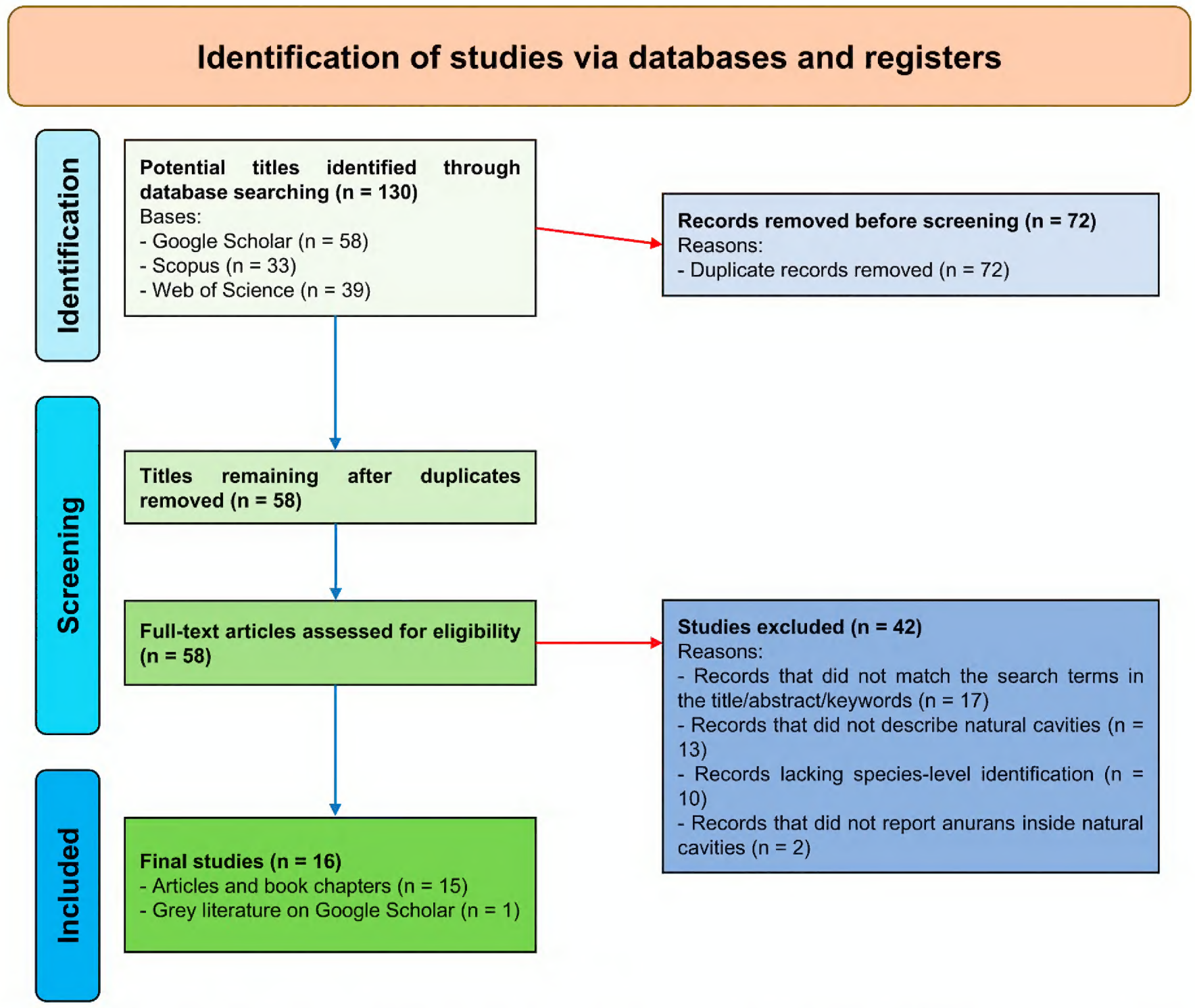
Identification of studies via databases and registers
Identification
Potential titles identified through database searching (n = 130)
Bases:
- Google Scholar (n = 58)
- Scopus (n = 33)
- Web of Science (n = 39)
Records removed before screening (n = 72)
Reasons:
- Duplicate records removed (n = 72)
Screening
Titles remaining after duplicates removed (n = 58)
Full-text articles assessed for eligibility (n = 58)
Studies excluded (n = 42)
Reasons:
- Records that did not match the search terms in the title/abstract/keywords (n = 17)
- Records that did not describe natural cavities (n = 13)
- Records lacking species-level identification (n = 10)
- Records that did not report anurans inside natural cavities (n = 2)
Included
Final studies (n = 16)
- Articles and book chapters (n = 15)
- Grey literature on Google Scholar (n = 1)

Figure 1. Prisma flow chart (Page et al. 2021) summarizing the selection of records of anurans observed within natural cavities in Brazil used in this review.

observations despite substantial sampling effort, exhibiting restricted distribution, low density, or highly cryptic behavior; Haddad et al. 2008).

The life history variables considered were length (for adult anurans, corresponding to the snout–vent length; Haddad et al. 2008; Vaz-Silva et al. 2020), represented in this study by the average length of adult males, females, or combined males/females and classified as small (≤ 49 mm), medium (50–99 mm), and large (≥ 100 mm), activity period (classified in this study as diurnal, nocturnal, or diurnal/nocturnal), habit and habitat (describing the species' niche and morphological and behavioral adaptations for survival, adapted from Haddad et al. 2008), and reproduction site (the reproductive strategies adapted from Haddad et al. 2008; Table 1). Data related to geographic distribution and life history were obtained from Haddad et al. (2008), Freitas (2015), Pezzuti et al. (2019), Magalhães et al. (2020), and Vaz-Silva et al. (2020).

Data analysis

The 177 records of anuran species from Brazilian caves, along with data on their conservation status, geographic distribution, and life history (Suppl. material 1), were organized into a matrix for statistical analysis. The data matrix

Table 1. Anuran species recorded in Brazilian caves, grouped by family (177 records in total). The number of species, the cumulative number of records in which each species was mentioned, and the species code are indicated. The complete and original data can be found in Suppl. material 2.

Count	Family	Species	Code	Number of records
1	Dendrobatidae	*Adelphobates galactonotus*	Adegal	1–2
2	Aromobatidae	*Allobates marchesianus*	Allmar	3
3	Dendrobatidae	*Ameerega flavopicta*	Amefla	4–6
4	Hylidae	*Boana albopunctata*	Boaalb	7
5	Hylidae	*Boana boans*	Boaboa	8
6	Hylidae	*Boana faber*	Boafar	9
7	Hylidae	*Bokermannohyla hylax*	Bokhyl	10–14
8	Hylidae	*Bokermannohyla martinsi*	Bokmar	15–29
9	Cycloramphidae	*Cycloramphus eleutherodactylus*	Cycele	30–35
10	Hylidae	*Dendropsophus nanus*	Dennan	36
11	Craugastoridae	*Haddadus binotatus*	Hadbin	37–38
12	Hylodidae	*Hylodes cardosoi*	Hylcar	39
13	Hylodidae	*Hylodes heyeri*	Hylhey	40
14	Brachycephalidae	*Ischnocnema guentheri*	Iscgue	41
15	Brachycephalidae	*Ischnocnema izecksohni*	Iscize	42
16	Brachycephalidae	*Ischnocnema juipoca*	Iscjui	43–48
17	Brachycephalidae	*Ischnocnema manezinho*	Iscman	49–55
18	Leptodactylidae	*Leptodactylus flavopictus*	Lepfla	56
19	Leptodactylidae	*Leptodactylus labyrinthicus*	Leplab	57–63
20	Leptodactylidae	*Leptodactylus latrans*	Leplat	64
21	Leptodactylidae	*Leptodactylus macrosternum*	Lepmac	65–66
22	Leptodactylidae	*Leptodactylus mystacinus*	Lepmys	67–72
23	Leptodactylidae	*Leptodactylus paranaru*	Leppar	73
24	Leptodactylidae	*Leptodactylus pentadactylus*	Leppen	74–75
25	Leptodactylidae	*Leptodactylus syphax*	Lepsyp	76–77
26	Leptodactylidae	*Leptodactylus troglodytes*	Leptro	78
27	Leptodactylidae	*Leptodactylus vastus*	Lepvas	79–82
28	Craugastoridae	*Oreobates antrum*	Oreant	83–84
29	Craugastoridae	*Oreobates heterodactylus*	Orehet	85–87
30	Phyllomedusidae	*Phyllomedusa burmeisteri*	Phybur	88
31	Leptodactylidae	*Physalaemus cuvieri*	Phycuv	89–95
32	Leptodactylidae	*Physalaemus ephippifer*	Phyeph	96
33	Leptodactylidae	*Physalaemus nattereri*	Phynat	97
34	Pipidae	*Pipa carvalhoi*	Pipcar	98
35	Craugastoridae	*Pristimantis fenestratus*	Prifen	99–103
36	Odontophrynidae	*Proceratophrys boiei*	Proboi	104
37	Bufonidae	*Rhaebo guttatus*	Rhagut	105–107
38	Bufonidae	*Rhinella crucifer*	Rhicru	108–110
39	Bufonidae	*Rhinella diptycha*	Rhidip	111–116
40	Bufonidae	*Rhinella granulosa*	Rhigra	117
41	Bufonidae	*Rhinella icterica*	Rhiict	118–119

Count	Family	Species	Code	Number of records
42	Bufonidae	*Rhinella magnussoni*	Rhimag	120
43	Bufonidae	*Rhinella marina*	Rhimar	121–122
44	Bufonidae	*Rhinella ornata*	Rhiorn	123–129
45	Bufonidae	*Rhinella rubescens*	Rhirub	130–136
46	Bufonidae	*Rhinella margaritifera*	Rhimarg	137
47	Hylidae	*Scinax catharinae*	Scicat	138–140
48	Hylidae	*Scinax eurydice*	Scieur	141
49	Hylidae	*Scinax fuscovarius*	Scifus	142–159
50	Hylidae	*Scinax ruber*	Scirub	160
51	Hylidae	*Scinax x-signatus*	Scixsi	161–166
52	Cycloramphidae	*Thoropa megatympanum*	Thomeg	167–168
53	Cycloramphidae	*Thoropa miliaris*	Thomil	169–174
54	Cycloramphidae	*Thoropa taophora*	Thotao	175–177

included two response variables (species and families) and 10 explanatory variables, with two related to conservation status, three to geographic distribution, and five to life history (Fig. 2).

Each variable category, both response and explanatory, was replaced with a sequential numeric code, and in cases where data for explanatory variables were missing, the category "not described (ND)" was also converted into a numeric code. Before analysis, the Variance Inflation Factor (VIF) was calculated to assess multicollinearity among the explanatory variables (cut-off threshold $VIF \leq 10.0$; Hair et al. 2019). Subsequently, the data were submitted to a redundancy analysis (RDA), a multivariate statistical method suitable for relating matrices of explanatory and response variables (Legendre and Legendre 2012). Analyses were performed using PAST software (version 5.3; Hammer et al. 2001) and the Rcmdr package (Fox 2005) in R software (R Core Team 2025).

Results

The 177 records of anurans from Brazilian Neotropical caves resulted in 54 species (Table 1). Redundancy analysis indicated that three variables related to conservation status and geographic distribution (IUCN conservation status, distribution area, and endemism) explain the occurrence of anuran species in Brazilian caves (31.1% of the variance explained by the first two axes; 27.0% of the total variance explained by the explanatory variables; $p = 0.001$; Table 2; Suppl. material 2).

Nine anuran species are associated with different IUCN conservation statuses, with a predominance of the "Least Concern" status (*Adelphobates galactonotus* Steindachner, 1864; *Allobates marchesianus* Melin, 1941; *Ameerega flavopicta* Lutz, 1925; *Boana albopunctata* Spix, 1824; *Boana boans* Linnaeus, 1758; *Boana faber* Wied-Neuwied, 1821; *Bokermannohyla hylax* Heyer, 1985; *Cycloramphus eleutherodactylus* Miranda-Ribeiro, 1920) compared to the "Vulnerable" status (*Bokermannohyla martinsi* Bokermann, 1964; Fig. 2).

Five species are related to area distribution and endemism, but with different combinations: non-endemic with extensive distribution area (*Scinax ruber* Laurenti, 1768; *Scinax x-signatus* Spix, 1824), endemic with extensive distribution

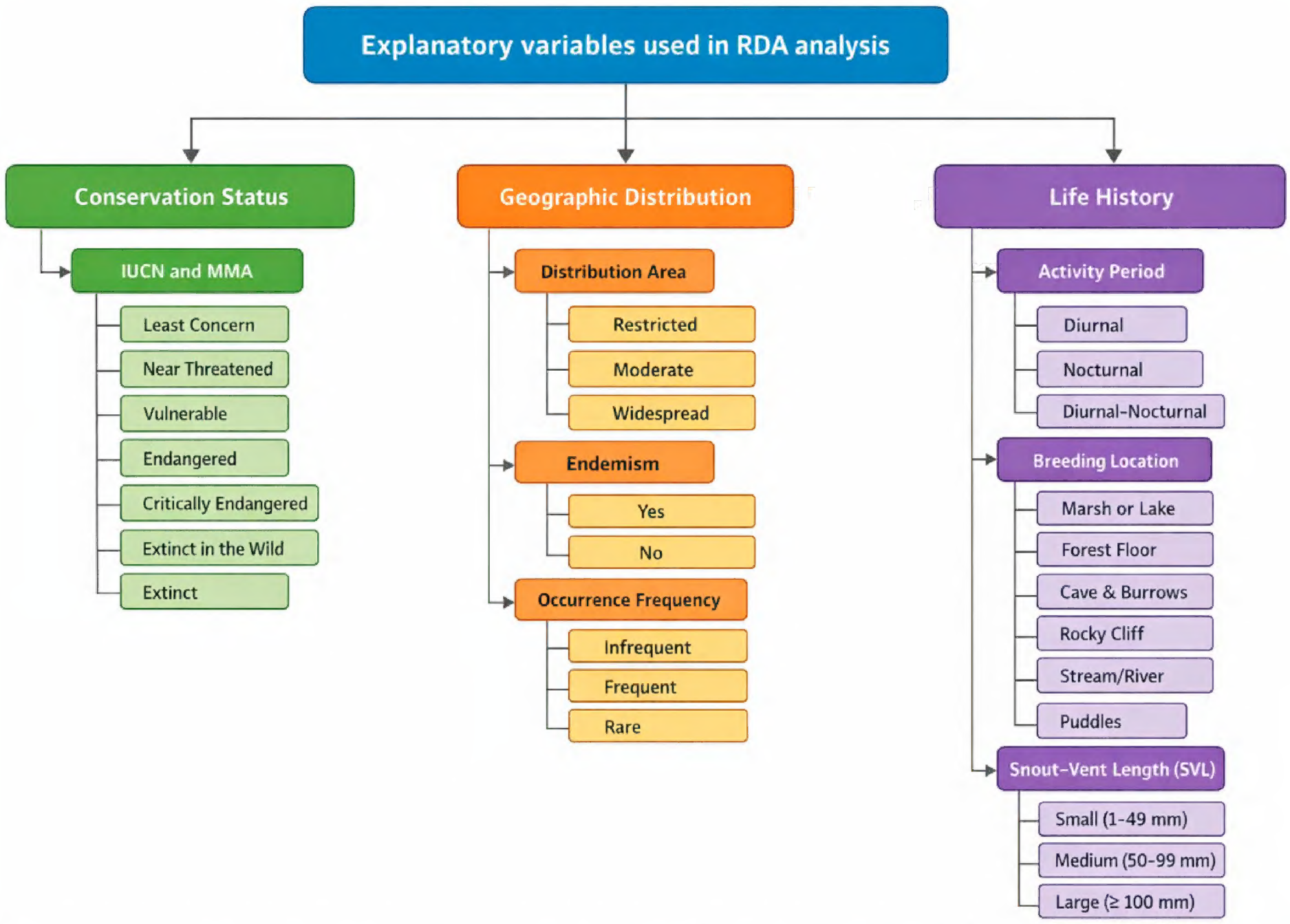

Figure 2. Categories of explanatory variables extracted from the anuran species recorded in Brazilian caves. IUCN = International Union for Conservation of Nature Red List status; MMA = classification by the Brazilian Ministry of the Environment.

area (*Thoropa miliaris* Spix, 1824; *Thoropa taophora* Miranda-Ribeiro, 1923), and endemic with restricted distribution area (*Thoropa megatympanum* Caramaschi & Sazima, 1984; Fig. 3).

Discussion

The results demonstrate that the occurrence of anuran species in Neotropical natural caves is primarily influenced by geographic variables, including IUCN conservation status, distribution area, and endemism. These patterns suggest that certain species are more capable of using subterranean environments than others. Ecological filters, such as habitat preferences and range size, likely shape cave communities. Overall, these findings emphasize the importance of geographic and conservation factors in understanding anuran ecology in caves.

The IUCN conservation status variable indicates that widely distributed species classified as “Least Concern” tend to occur more frequently in the natural caves considered. Considering all occurrence records compiled from the literature, most were classified as Least Concern, representing 94.3% of the records according to both the IUCN and the Brazilian Ministry of the Environment (MMA). A smaller proportion corresponded to threatened categories, including Vulnerable (3.5%) and Endangered (1.5%) in the IUCN classification, while the MMA classification included Near Threatened (3.5%) and Endangered (1.5%), with 0.7% of records not evaluated. Eight species were associated with this

Table 2. Results of the redundancy analysis (RDA) ordination examining the relationship between explanatory variables and anuran species and their families (response variables) recorded in the scientific literature for Brazilian caves. (A – ordination metrics) Eigenvalues, explained variance (%), and correlations (*r*) by axis. (B – explanatory variables) Scores and variance inflation factors (*VIF*) of explanatory variables. (C – model summary) Statistical summary of the RDA model. IUCN = International Union for Conservation of Nature Red List status; MMA = classification by the Brazilian Ministry of the Environment.

		Axis 1	Axis 2	VIF
A	Eigenvalue	82.9	2.4	–
	Axis %	30.2	0.9	–
	Cumulative %	30.2	31.1	–
	r	0.6	0.6	
B	IUCN	0.40	0.01	2.17
	MMA	0.07	0.01	1.51
	Distribution area	−0.37	−0.03	2.57
	Endemic	−0.39	−0.03	1.45
	Frequency	−0.04	0.02	1.28
	Snout–vent length	−0.02	0.01	1.49
	Activity period	0.02	−0.02	1.13
	Habit	0.14	0.00	1.61
	Habitat	-0.09	0.01	1.59
	Breeding location	0.04	0.08	1.82
C	R^2	0.270		
	F	7.492		
	p	**0.001**		

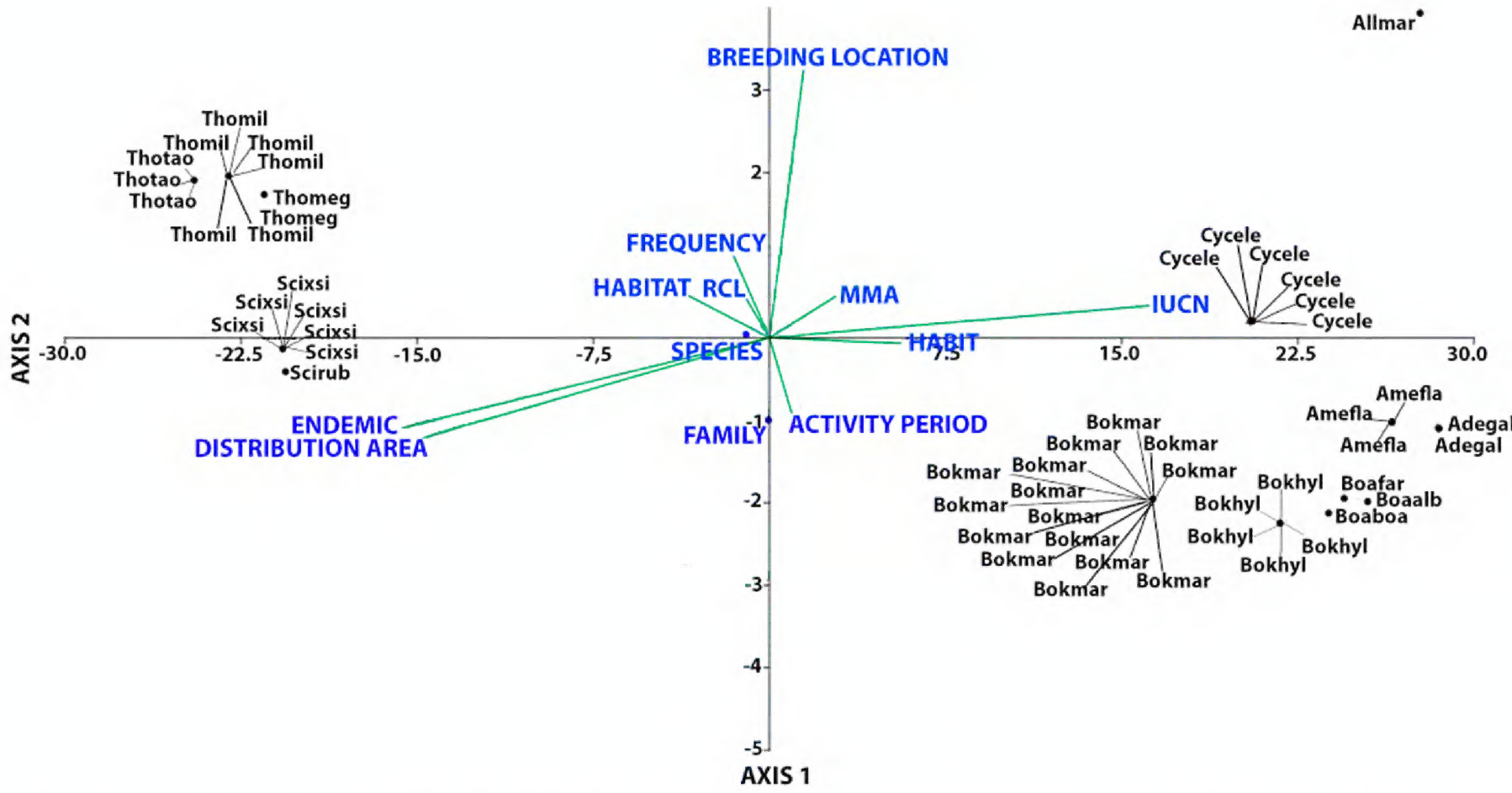

Figure 3. Redundancy analysis (RDA) ordination diagram displaying the association between anuran species and their families (response variables) recorded in Brazilian caves and the explanatory variables. Only species with scores above ±20 are shown (black points). Species codes correspond to those listed in Table 1.

variable, suggesting that the anurans recorded in caves comprise species with sufficient quantifiable information, indicating that they are abundant, widely distributed, and face no or low risk of extinction (IUCN 2024). A wide geographic distribution suggests that the species exhibit low niche specificity; that is, they can occupy heterogeneous environments and present greater ecological plasticity. In this case, this plasticity includes caves as shelter, reproductive sites, or refuge against unfavorable conditions (Eterovick et al. 2010; Matavelli et al. 2015; Sperandei et al. 2023). This would be the case for species *A. flavopicta*, *C. eleutherodactylus*, and *B. boans*, which utilize heterogeneous microhabitats such as rock crevices, small holes in slopes, tree trunks, and bromeliad rosettes. These microhabitats are indicative of microclimatic conditions similar to those found inside caves (Lima et al. 2012a, 2012b; Martins and Giaretta 2012). In contrast, species *A. galactonotus*, *A. marchesianus*, *B. albopunctata*, *B. faber*, and *B. hylax* are widely distributed and occupy varied microhabitats, ranging from areas associated with accumulated leaf litter (e.g., *A. marchesianus*) to sites near water bodies (*A. galactonotus*, *B. faber*, and *B. hylax* during the breeding season) (Haddad et al. 2008; Vaz-Silva et al. 2020). These environments provide indirect evidence of conditions that may occur in the subterranean habitat and thus suggest the potential for habitat occupation (Juncá and Eterovick 2007; Carvalho et al. 2012; Luza et al. 2015; Medeiros et al. 2024).

On the other hand, only one species classified as "Vulnerable" (*Bokermannohyla martinsi*) is associated with the IUCN conservation variable. This classification is characterized by a reduction of at least 30% in the adult population over the last 10 years or three generations due to habitat degradation, a restricted geographic distribution with continuous decline or marked fragmentation, and a small population of mature individuals (>10,000 individuals) or a very small or restricted population (<1,000) that is declining (IUCN 2024). However, the low incidence of vulnerable species in caves may be due to their inherent rarity, which reduces their probability of detection in biospeleological studies.

Geographic distribution and endemism proved to be important variables for the separation of the ordination axes in the analysis, with five species associated with these characteristics. The formation of three distinct patterns was observed: (i) non-endemic and widely distributed species, such as *Scinax ruber* and *S. x-signatus* (Pinto da Rocha and Sessegolo 2001; Donato 2011); (ii) endemic species with relatively wide distribution, such as *Thoropa miliaris* and *T. taophora* (Matavelli et al. 2015; Dos Santos et al. 2022); and (iii) endemic and restricted-distribution species, such as *T. megatympanum* (Dos Santos et al. 2022). This differentiation suggests that, although the capacity to occupy subterranean environments is relatively broad among anurans and they are physiomorphologically capable of inhabiting cave environments (Sperandei et al. 2023, 2025), the use of caves does not occur homogeneously across species with different biogeographic patterns. Endemic species tend to exhibit greater environmental specificity or dependence on particular microhabitats (Haddad et al. 2008; Vaz-Silva et al. 2020). This may explain their presence in caves within the species' restricted range. Endemic species that exhibit wide distribution, as is the case for *Thoropa miliaris* and *T. taophora* in this study, are often associated with human-impacted or heterogeneous environments. They may access caves opportunistically or seasonally, particularly during periods of water or thermal stress in the external environment (Bernarde 2012; Luría-Manzano et al. 2017; Sperandei et al. 2023).

Among the non-endemic, widely distributed species are anurans of the family Hylidae (*S. ruber* and *S. x-signatus*). These taxa are frequently associated with environments with varied conditions, including anthropized open areas and vegetation edges, as well as dense and preserved forest areas (Anunciação et al. 2023). This variability favors the opportunistic occupation of caves in different localities, especially as a temporary shelter or refuge against unfavorable external conditions. This behavior is consistent with widely documented patterns for generalist hylid species, which exhibit high environmental tolerance and ease of dispersal (Anunciação et al. 2023).

Although the predominance of Least Concern species in the records may reflect broad patterns of distribution and ecological tolerance, the presence of more restricted species, such as *Thoropa megatympanum*, indicates that certain taxa with more specific ecological niches also inhabit caves. *T. megatympanum* is endemic to rupestrian areas of the Serra do Espinhaço (Minas Gerais) and exhibits a set of life history traits narrowly associated with rocky microhabitats with a water film, where vocalization, oviposition, and larval development activities occur (Leite et al. 2019). Studies on the genus *Thoropa* show that these species deposit their eggs adhered to humid surfaces, and their tadpoles have developed adaptations to water films and shallow layers on rock, which demand high humidity stability and surface microhydrology (Caramaschi and Sazima 1983; Giaretta and Facure 2004). This set of adaptations suggests that the presence of *T. megatympanum* in caves may be less related to ecological generalism and more to the availability of suitable rupestrian microhabitats within or in the vicinity of the caves, which explains its differentiated positioning in the RDA analysis among endemic and restricted-distribution species.

Variables directly related to the animals' life history (including activity period, habitat, habits, breeding site, and body size) contributed little to the model's explained variance and were not selected as determinants of anurans' presence in the subterranean environment. This pattern may reflect not only ecological processes but also methodological limitations associated with the availability and quality of life-history data for many Neotropical species. Life-history traits are often incompletely described or inconsistently reported in the literature, which can reduce their explanatory power in macroecological analyses. This result suggests that the occupation of caves by anurans in the Neotropical environment is less dependent on physiological or behavioral attributes and more on the geographic–ecological context of each species. Thus, the use of caves by anurans follows an opportunistic pattern, in which generalist, widely distributed, and non-threatened species use these environments as a refuge or complement to the surface niche, corroborating studies reported in other tropical regions (Suwannapoom et al. 2018; Couto et al. 2023).

Finally, the low contribution of life-history variables may indicate that cave use by anurans is not strongly structured by species-specific life-history traits but rather by opportunistic use of subterranean habitats as temporary refuges. In this sense, caves may function primarily as microhabitats that provide stable environmental conditions, such as higher humidity and protection from predators, allowing different species with distinct ecological traits to exploit these environments. However, limited standardization in the collection and reporting of life-history information in biospeleological studies still restricts the availability of consistent ecological data for many species occurring in subterranean

environments. Since these species are not mandatory targets for collection or monitoring under current legislation, records tend to be sporadic, which may reduce the ability to detect broader ecological patterns at larger spatial scales. Additionally, the available literature may present regional sampling biases, with certain areas of Brazil being more intensively surveyed than others, which can influence the distribution of records compiled in this review. Such biases, together with variation in sampling effort and detectability among studies, should be considered when interpreting macroecological patterns derived from published occurrence data. Even so, the results indicate that anurans' cave occupation may be more closely associated with environmental opportunism than with specific life-history strategies, reinforcing the importance of subterranean environments as complementary habitats in the ecology of these amphibians (Trajano and Bichuette 2006; Silva et al. 2012).

Conclusion

The patterns reported herein suggest that the occurrence of anurans in Neotropical caves primarily reflects opportunistic use of subterranean habitats, driven by ecological plasticity and characterized by widespread, generalist species rather than specialized or rare taxa. Nevertheless, caves can provide supplementary shelter or breeding sites under variable environmental conditions, highlighting their role as complementary habitats. Future research should focus on systematic surveys and long-term monitoring to better understand the ecological drivers of cave use, thereby informing conservation actions to protect subterranean habitats and the species that rely on them. From a management perspective, these findings highlight the importance of including anuran surveys in environmental licensing procedures and speleological inventories, since these species are often recorded opportunistically and are not currently mandatory targets in many cave monitoring programs. Methodological advances such as acoustic monitoring, environmental DNA (eDNA) detection, and genetic comparisons between cave and surface populations may also provide valuable insights into patterns of habitat use, detectability, and population connectivity in subterranean environments.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

This research did not involve animal handling; thus, no ethical approval was required.

Use of AI

No use of AI was reported.

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Author contributions

Vinícius Sperandei: conceptualization, investigation, methodology, figure preparation, and writing original draft; Wilian Vaz-Silva: writing critical review; Cássio Cardoso Pereira: figure preparation and writing critical review; Francisco Leonardo Tejerina-Garro: supervision, investigation, methodology, and writing critical review.

Author ORCIDs

Vinícius da Fontoura Sperandei https://orcid.org/0000-0002-3093-706X
Wilian Vaz-Silva https://orcid.org/0000-0001-6235-5331
Cássio Cardoso Pereira https://orcid.org/0000-0002-6017-4083
Francisco Leonardo Tejerina-Garro https://orcid.org/0000-0002-5159-8108

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Independent records of anurans in underground cavities found in scientific publications from 1980 to 2022, and biological and natural history characteristics

Authors: Vinícius da Fontoura Sperandei, Wilian Vaz-Silva, Cássio Cardoso Pereira, Francisco Leonardo Tejerina-Garro

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Supplementary material 2

Complete results for the 4 axes demonstrated by RDA for the analyzed records and variables

Authors: Vinícius da Fontoura Sperandei, Wilian Vaz-Silva, Cássio Cardoso Pereira, Francisco Leonardo Tejerina-Garro

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